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Research Document 2004/107 | **Document de recherche 2004/107**

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Changes in the Reproductive Parameters of Female Harp Seals (*Pagophilus groenlandicus*) in the Northwest Atlantic

Changements dans les paramètres de reproduction des femelles du phoque du Groenland (*Phoca groenlandicus*) de l'Atlantique Nord-Ouest

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ISSN 1499-3848 (Printed / Imprimé)
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Abstract

Reliable data on harp seal (*Phoca groenlandicus*) fertility rate, age specific pregnancy rates and mean age of sexual maturity are required to understand the population dynamics of this species and to provide a sound scientific base for the development of a sustainable management plan. The objectives of this manuscript are to examine changes in female reproductive parameters from 1980 – 2001 as well as long-term trends since the early 1950s. Estimates of the total number of harp seals in the Northwest Atlantic declined from approximately 3.0 million in the 1950s to 1.8 million in the early 1970s and then increased steadily to 5.2 million in 1996 where it has since stabilized. During this period, annual fertility rates increased from approximately 86% in the 1950s to a high of 98% in the mid 1960s and then declined steadily to approximately 65-70% by the early 1990s where it has stabilized. Concurrently, the mean age of sexual maturity decreased from 5.8 years in the mid 1950s to 4.1 in the early 1980s, then increased to 5.3 years by the early 1990s and peaked at 5.7 years by 1995. In 2001 the mean age was approximately 5.3 years. Although the direction of change in each of the reproductive parameters examined was consistent with a density dependent response, changes in population size explained very little of the variability observed in ovulation rates and mean age of sexual maturity. Given the current formulation of the harp seal population model, pregnancy rates were not independent from population size and could not be tested statistically, but there was a significant year effect. These data suggest other ecological or environmental factors may be important; possible implications of changing oceanographic conditions in the Northwest Atlantic are discussed.

Résumé

On a besoin de données fiables sur le taux de fécondité du phoque du Groenland (*Phoca groenlandicus*), sur les taux de conception par âge et sur l'âge moyen à la maturité sexuelle pour comprendre la dynamique des populations de l'espèce et pour avoir de bons fondements scientifiques pour élaborer un plan de gestion durable. Les changements dans les paramètres de reproduction des femelles de 1980 à 2001, ainsi que les tendances à long terme depuis le début des années 1950, sont examinés dans ce rapport. Les estimations du nombre total de phoques du Groenland dans l'Atlantique Nord-Ouest sont passées d'environ 3,0 millions dans les années 1950 à 1,8 million au début des années 1970. Elles ont ensuite augmenté de façon constante pour atteindre 5,2 millions en 1996 où elles sont demeuré stable. De leur côté, les taux de fécondité annuels, qui étaient d'environ 86 % au début des années 1950, ont culminé à 98 % au milieu des années 1960, pour ensuite redescendre de façon régulière jusqu'à environ 65 à 70 % au début des années 1990, lorsqu'ils se sont finalement stabilisés. Simultanément, l'âge moyen à la maturité sexuelle est passé de 5,8 ans au milieu des années 1950 à 4,1 ans au début des années 1980, pour ensuite augmenter à 5,3 ans au début des années 1990, et atteindre un pic de 5.7 ans en 1995. En 2001, l'âge moyen était d'environ 5,3 ans. Même si le sens du changement dans chacun des paramètres de reproduction examinés correspondait à une réaction dépendante à la densité, les changements dans la taille de la population expliquent très peu la variabilité observée dans les taux de fécondité et l'âge moyen à la maturité sexuelle. En raison de la conception actuelle du modèle de la population de phoque du Groenland, les taux de conception ne sont pas indépendants de la taille de la population et ne peuvent pas être vérifiés statistiquement, bien que l'effet de l'année était important. Ces données laissent supposer l'existence d'autres facteurs écologiques ou environnementaux d'importance. On discute ensuite des conséquences possibles des changements observés dans les conditions océanographiques régnant dans l'Atlantique Nord-Ouest.

Introduction

The harp seal, *Pagophilus groenlandicus*, is an abundant, migratory species distributed throughout most of the north Atlantic. There are three populations identified on the basis of breeding location, these include the Northwest Atlantic population, the White Sea/Barents Sea population and the Greenland Sea population. The Northwest Atlantic population is the largest and breeds in two locations, the Northeast coast of Newfoundland and in the southern Gulf of St. Lawrence. The traditional migration pattern and timing of harp seal movements in Newfoundland and Labrador waters has been described by Sergeant (1965, 1991). During the summer most animals are in Arctic waters feeding heavily in areas as far north as Thule in Northwest Greenland and as far west as Barrow Strait in the Canadian Arctic as well as into Hudson Bay. In late October and November, herds migrate southward along the coast of Labrador; the Newfoundland component of the population disperses across the Grand Banks and shelf-edge area while the Gulf of St. Lawrence component moves through the St. of Belle Isle enroute to the southern Gulf. Seals continue to feed until late February after which time they form large aggregations on the ice to pup and mate. After mating, female seals disperse to feed and then haul-out on the ice in large herds in late April and May to moult; the northward migration into more northern waters occurs in June.

Harp seals have been hunted commercially since the mid eighteenth century but the height of the sail and wooden steamer fishery occurred in the mid nineteenth century when catches peaked at close to 450,000 seals/year (Sergeant 1991). By the early 1900s with the introduction of the first steel-hulled steamers, catches had declined to approximately 250,000 seals/year. During the First World War and the interwar period catches declined further and then came to a halt at the beginning of the Second World War. However, from 1950 – 1971 the fishery was revived, in part due to Norwegian participation, and catches increased rapidly to an average of 288,000 seals/year. The first total allowable catch (TAC) was set in 1971 and it remained at 175,000 animals from 1972 – 1982. The average catch of seals during this time period was 165,000. In 1983, the European Economic Community banned the importation of young harp seal (whitecoat) pelts which eliminated the market for seal products and ended the traditional large-vessel commercial seal hunt. From 1983 – 1995 catches remained low averaging 52,000 seals/year; however, in 1996, the TAC was increased to 250,000 and then to 275,000 in 1997. This increase was in response to a revitalized pelt market and the development of new seal oil markets. From 1996 – 2001, catches increased to greater than 240,000 seals/year with the dominant age class taken being young of the year that have moulted their whitecoat ('beaters'). The current management plan allows a quota of 975,000 harp seals to be taken over a three year period with a maximum of 350, 000 in any one year (DFO 1995; 2000a; 2002).

There have been several models developed over the years to estimate the total population of harp seals in the Northwest Atlantic (Lett and Benjaminsen 1977; Lett *et al.* 1978; Winters 1978; Roff and Bowen 1983; Shelton *et al.* 1995; Healey and Stenson 2000). Although some studies have taken different modeling approaches, it is generally believed that the number of harp seals declined during the postwar commercial seal hunt from approximately 3 million in 1952 to 1.8 million in the early 1970s. Following the imposition of the first TAC, the population increased throughout the 1970s and early 1980s. With the demise of the large vessel hunt in 1983, catches were further reduced and the population increased to an estimated 4.3 million seals in 1990 and then to 4.9 million seals in 1994 (Healey and Stenson 2000). The current population estimate, based on a pup production survey conducted in 1999, is 5.2 million seals (95% CI 4.0 – 6.4 million) and it appears that growth of the Northwest Atlantic population has stabilized since 1996 (Healey and Stenson 2000).

These significant changes in the size of the Northwest Atlantic harp seal population have been accompanied by changes in the long-term reproductive potential of females (Bowen *et al.* 1981; Sergeant 1991). Fertility rate, age-specific pregnancy rates and mean age of sexual maturity are of particular importance for modeling and understanding the dynamics of this population as well as providing the scientific basis for a sustainable management and resource use plan. Several authors have suggested that one, or a combination of these reproductive parameters, have varied in a density dependant manner from the 1950s to the early 1980s. Sergeant (1966, 1973, 1976, and 1978) and Winters (1978) suggested that mean age of whelping declined concurrently with population size, but that the pregnancy rate of older females (aged 8+) had not changed. Lett and Benjaminsen (1977) and Lett *et al.* (1978) presented evidence that both parameters changed with the declining population. Bowen *et al.* (1981) reviewed and reanalyzed all available data and concluded that both mean age of sexual maturity and fertility rate changed significantly as the population declined. Mean age of sexual maturity declined from approximately 6.2 yr in 1952 to 4.5 in 1979. During the same period fertility rate increased from 85 to 95%. Bowen *et al.* (1981) considered it likely that density-dependent mechanisms were involved, but emphasized sufficient empirical data were still lacking. Rivard (1978) as well as Bowen *et al.* (1981) pointed out that our understanding of any density-dependent relationship was unlikely to improve until the harp seal population increased to a high level sometime in the future.

The Northwest Atlantic harp seal population is currently at the highest level ever recorded and data from 1980 to the present are available (Sjare et al. 2000) to examine how reproductive parameters have varied with increasing population size. However, during this same time period the marine environment has also undergone significant change. For example, an increased volume of cold water flowed on to the northern and southern Grand Banks of Newfoundland from the Labrador Current during the late 1980s until the mid 1990s (Carscadden *et al.* 2001; Drinkwater 1996; 2000; 2002). The colder than normal water temperatures

are thought to be, at least in part, responsible for significant changes in the biomass, distribution, habitat use, timing of migration and reproductive biology of numerous, seabird and marine mammal species (Parsons and Lear 2001; Lilley and Carscadden 2002; Rice 2002). Although water temperatures have now returned to the 20-year norm, many biological components of the ecosystem have not, emphasizing the complex and poorly understood nature of these large scale changes. The objectives of this manuscript are to present data collected on reproductive parameters from 1980 -2001 as well as provide a more detailed interpretation of longer-term changes in these parameters since the early 1950s relative to changing population abundance and a changing marine environment.

Materials and Methods

Female reproductive tracts and jaws have been collected from harp seals in most areas of Newfoundland and southern Labrador since 1980 and 1985, respectively, and during all times of the year except summer (a time when most animals have migrated into more northern waters). The most consistently sampled area is the Northeast coast of Newfoundland between November and May. During this time period, the biological collection program involved 20 – 45 experienced seal hunters from around the province as well as technical and research personnel from the Department of Fisheries and Oceans (DFO). Many of the hunters have participated in the program for numerous years and have provided both continuity and consistency to the sampling program. Historic data collected prior to 1980 were obtained from Bowen *et al.* (1981) and are based on samples collected primarily in Northeast Newfoundland during the spring (late March-April) or winter (January-February). Details pertaining to the origin and author source of these data are given in Bowen *et al.* (1981; Table 1 and 2).

Seal ages were determined to the nearest year by sectioning a lower canine tooth and then counting dentine annuli (Fisher 1954). The reproductive status of females was assessed by examining the ovaries and uterus (Fisher 1954; Bowen *et al.* 1981). Reproductive tracks were either preserved in 5% formalin or frozen; ovaries were cut into 2.0 mm thin serial sections for examination. Females were considered immature if the ovaries were small and contained only inactive follicles with no corpus luteum (CL) or corpus albicans (CA). If there was evidence of a CL and/or CA in either ovary then the seal was considered to be mature. Mature females sampled in the late fall and winter were designated as pregnant or non-pregnant based on the presence or absence of a large, fully luteinized CL in one of the ovaries, and since 1990, evidence of a developing fetus and an enlarged, ruggose uterus. Non-pregnant females in the late fall and winter lacked an active CL, but showed evidence of having ovulated previously (i.e. a CA present).

Fertility rate was defined as the percentage of mature females pregnant at the time of sampling. Age specific pregnancy rates were defined as the percentage of females pregnant in a particular age class regardless of maturity

status. The blastocyst in harp seals does not implant until approximately 3 months after fertilization so fertility rate and age specific pregnancy rates are most reliably determined from females sampled in the fall and winter when females are carrying late-term fetuses. Therefore, only fall and winter samples were used to estimate the above mentioned parameters. Ovulation rate was defined as the percentage of mature females that had ovulated at the time of sample; April and May samples were used to estimate ovulation rate.

When possible, information on female harp seal reproductive parameters were summarized and presented annually from 1954 to 2001. However, total annual sample sizes ranged considerably and age-specific samples were highly variable with no data for many year-age combinations. To address these problems, Healey *et al.* (2000) used a non-parametric regression estimator with a Gaussian weight function to predict annual age specific pregnancy rates from the sample data. In order to predict rates for seals over the time series, observed rates were smoothed and sampling gaps were bridged by applying kernel smoothing. Bandwidths for smoothing were selected using the generalized cross-validation statistic (Hastie and Tibshirani 1990). Details on this analysis technique are documented in Appendix 1.

Population estimates from Healey and Stenson (2000) were used to evaluate long-term changes in reproductive parameters relative to changes in the size of the 1+ harp seal population (Figure 1). The model is age structured and uses independent survey estimates of pup production, annual estimates of age specific pregnancy rates and removals (eg. by-catch and seals 'struck and lost'). It is important to note that this version of the population model provides estimates from 1960 – 2000. Therefore, although this manuscript summarizes and presents data from the mid 1950s, they are not included in any of the regression analyses examining long-term changes. This limitation should also be kept in mind when evaluating analyses that regressed MAM against lagged 1+ population estimates.

Mean and variance of age at sexual maturity was calculated following DeMaster (1978; 1984) using a life table approach. The relevant statistic for this method is the age-specific probability that an individual female first matured. These probabilities are calculated from the age-specific maturity rates. In cases where the estimated age-specific maturity rates decreases from one age to the next older, the number of females maturing at the specific age in question is actually calculated to be negative. A number of approaches have been suggested to address this problem. Bowen *et al.* (1981) smoothed data across the ages where declines had occurred in the age-specific maturity rate and assumed that age-specific probabilities of first maturing were normally distributed in making this interpolation. We attempted a similar correction using linear interpolation, but found that the technique did not perform well at low sample sizes. A simpler alternative, and the one used in this analysis, was to assume that age-specific maturity rates could not decrease in older age classes, so in cases where it did,

the higher value from the younger age class was used. This method appeared to perform well in all scenarios, even when sample sizes were low.

Ovulation rates, fertility rates, and age specific pregnancy rates were all analysed similarly as binomially distributed data. Logistic regressions were conducted to analyze trends in rates over years or with lagged population sizes (usually 1+ population size lagged 1 year). Linear regressions were used to test for relationships between year and population sizes (with various lags) and mean age at sexual maturity. As only mean and calculated variances were available (not the 'raw' data) an adjustment was made to standard regression analyses to ensure that appropriate samples sizes and the variance in the mean age at sexual maturity was incorporated into the analysis. The variance-covariance matrix of mean age of sexual maturity and the predictor (calculated using PROC CORR in SAS) weighted by the sample size used in each year to calculate MAM was used by the regression as the input data (TYPE=COV in PROC REG). Further, the additional pooled variance in MAM was calculated by

$$\mathrm{var} = \frac{\sum^{t}(\mathrm{var}(t) * (\frac{n_t}{n_t - 1}))}{\sum^{t} n_t - 1} * \frac{\sum^{t}(\mathrm{var}(t) * n_t)}{\sum^{t} \mathrm{var}(t)}$$

where *t* is year, and was added to the variance in MAM in the variance-covariance matrix before conducting the regression.

Results

The long-term trend in ovulation rates of mature females is presented in Table 1. Annual rates remained higher than 96% until the mid 1980s then appeared to decrease to perhaps as low as 71% from 1988 – 1991. After this period, rates were again in the order of 95% but more variable. Small sample sizes during the late 1980s and early 1990s made it very difficult to determine the timing and the actual extent of this decrease. There was a significant regression of ovulation rate against year (X^2=4.92, d.f. = 1, P=0.027; Figure 2) and on the 1+population lagged by one year (X^2=4.10, d.f.=1, P=0.043; Figure 3)

Although there was year to year variation in fertility rates due to very small sample sizes in some years (particularly the 1980s), a long-term trend was discernable. In the mid 1950s when the population was at a postwar high, the fertility rate was 86%, it then increased to approximately 95% during the commercial whitecoat hunt in the mid 1960s and subsequently declined steadily to a low near 60% by the late 1990s; in 2000 and 2001 rates were approximately 70% (Table 2). There was a significant regression of fertility rate against year (X^2=186.10, P=0.0001; Figure 4). Because age specific pregnancy rates are an

input variable for the harp seal population model, the relationship between fertility rate and the size of the 1+ population is not independent and not presented here.

Annual, late term, age specific pregnancy rates for all females aged 3 to 7+ are presented in Table 3. There was considerable inconsistency in these data due to small sample sizes particularly from 1982-1986 as well as two major data gaps from 1954-1964 and from 1970-1978. Annual age specific pregnancy rates calculated using the Gaussian regression estimator for interpreting data gaps and kernel smoothing technique are presented in Table 4 and Figure 5. For seals aged 4 and 5 years old, the proportion pregnant began to gradually decline from the late 1950s until approximately 1965 at which time annual rates increased quickly until the late 1970s. In the case of 4 year seals, rates remained high until the early 1980s and then sharply declined to a low in the early 1990s; in recent years there has been little change from this level (Figure 5). Seals 5 years of age exhibited the same pulse of productivity except that rates remained high until the mid-1980s, and then appeared to decline more slowly to a low in the mid-1990s. The change in pregnancy rates of 6 and 7+ year old seals was notably less pulsed but rates still declined steadily during the mid 1980s and early 1990s and have remained low to the present (Figure 5). Note that Figure 5 and Table 4 were based on the output from an earlier but comparable run of the population model and were included here for discussion purposes (Healy *et al.* 2000).

The mean age of sexual maturity (MAM) declined from 5.8 years in the mid 1950s to a low of 4.1 years in 1979, it then increased to approximately 4.6 in 1987 and to a high of 5.7 in 1995 where it stabilized until 1999. By 2000 and 2001 MAM appeared to have declined to approximately 5.3 years (Table 5 and Figure 6). When MAM from 1962-1979 and from 1980-2001 were regressed against year both were significant but the R^2 was low in each of the analyses (Table 6a and b respectively). The results were similar when both sets of data were regressed against the 1+ population lagged by 5 and 10 years (Table 6a, and b). When MAM from the entire time series was regressed against the 1+population lagged 1 to 10 years, the results were significant due to large sample sizes but there was little biological relationship between the variables (Table 6c and Figure 7).

Discussion

Bowen *et al.* (1981) emphasized that the apparent density-dependent changes in MAM and fertility rate of harp seals in the Northwest Atlantic relied heavily on the sparse 1950s data. In addition, both he and Rivard (1978) realized that further understanding of these relationships would not improve until the population size had once again reached a high level sometime in the 1990s. Since the time of their studies, the seal population has grown at a rate of approximately 5 -7 % per year from 1980 -1996 and then stabilized at an estimated 5.2 million seals in 2000 (Healey and Stenson 2000). Although the changes in ovulation rates, fertility rates and MAM observed during this study were in the

direction expected for a density dependent response, there are problems with this interpretation for the post 1980 data.

Ovulation Rates,

Bowen *et al.* (1981) found no relationship between ovulation rates and 1+ population size from 1950 -1970. Data presented here suggests that rates dropped from 1986 – 1991 and then remained lower and more variable throughout the 1990s. Unfortunately, given the limited number of annual samples, it was difficult to document the timing and extent of the initial decline. However, given that rates appeared to remain lower and more variable from 1995 to 1999 this observation was probably not simply a sampling problem during the mid to late 1980s. However, data used to examine annual ovulation rates were collected during the spring and early summer period throughout the entire time series. Years when sample sizes were large (i.e. usually in excess of 100 animals) indicates that at least a portion of the sample was taken during a dedicated, DFO supported, research trip to the moulting patch. Sampling females to determine reproductive status during the moulting period can be problematic because there known to be sex and age segregations within the patch (Sergeant 1991). Males tend to haul-out approximately two weeks earlier than females and immature seals; younger seals may first haul-out in more peripheral areas of the aggregation and then gradually become more integrated with the main herd as the spring melt progresses. Since the late 1980s both the duration and timing of moulting trips designated for sampling have been planned to minimize these potential biases as much as possible.

The significant relationships between ovulation rates and the changing populations size observed over the entire time series are of interest because, in general, pinniped ovulation rates remain relatively constant for females in the prime of their reproductive except during 'extreme' climatic events and/or during severe food shortages (Boyd *et al.* 1999; Trillmich 1993). The observed decline and period of variability in ovulation rates in this study overlapped with changing oceanographic conditions in the Northwest Atlantic. So, although population size was increasing during this time period, it is possible that the colder than normal oceanographic ice conditions and subsequent changes in the marine environment were also contributing factors. Therefore, it is not possible to conclude that a density dependent response is the primary explanation for these data and observations.

Fertility and Age Specific Pregnancy Rates

Fertility rates varied from 86% during the post war population high to approximately 95% during the 1960s and early 1970s commercial hunt period. By 1980 rates began to decline and continued to do so throughout the 1990s to a low in the range of 70%. Although this pattern of change is consistent with a density dependent response, it was not possible to examine the statistical relationship

between fertility rates and changing population size because age specific pregnancy rates are one of the three input parameters used in the current population model, and therefore, fertility rate and size of the 1+ population are not independent variables Bowen *et al.* (1981) considered it likely that declining harp seal abundance and increasing fertility rates from 1954 – 1979 was evidence a density dependant response. However, this study can not confirm their conclusion because of the current formulation of the harp seal population model and the potential importance of large scale ecosystem changes since 1985. The significant relationship between fertility rate and year was strongly influenced by the lack of data from the mid 1950s and the steady post 1980 decline in rates during a time period when the population was growing at approximately 5 - 7% per year.

Interpreting annual fertility rates was challenging given the small sample sizes and the variability of data. Using only information from females in the late stages of pregnancy minimizes any biases in rates resulting from pseudo-pregnancy, embryo absorption and early-term abortion. However, small sample sizes introduce other potential problems. Although hunters participating in the biological collection program were instructed to spread out their hunting effort during the months of November – February each year and to take seals from numerous skulls passing through their hunting areas, it was not always possible given the weather and sea conditions. There is known to be some age segregation in the migratory behavior and habitat use of harp seals. In many areas older seals move southward into Newfoundland waters first (Sergeant 1991) and at certain times in the late fall and early winter younger seals frequent nearshore areas more that older seals (Sergeant 1991). If biological collections were consistently taken over a short time period during the fall migration and from restricted geographic regions of the Province, then biases in annual fertility rates could occur. The biological collection program, which has 20 to 45 hunters participating from numerous communities around the Province, was designed to alleviate this potential concern. However, the very limited amount of data from the 1980s could still be problematic from this perspective. Another potential problem relates to the assumption that most harp seals summering in Greenlandic and Arctic waters return annually to pup and/or breed off Newfoundland or in the Gulf of St. Lawrence. Recent observations in West Greenland suggest that there may be increased numbers of seals remaining in more northern waters until late winter or even throughout the entire winter (pers. comm. A. Rosing-Asvid, Greenland Fisheries Institute). If a significant proportion of these seals are non-pregnant or immature females, then annual fertility rates and age specific pregnancy rates based on seals collected only in Newfoundland and Labrador would be over-estimated and MAM would be under-estimated. At present there are no data to evaluate the seriousness of this potential problem, but it does warrant consideration in the future.

Fertility rates of 50 - 90% appear to be the norm for adult pinnipeds, but there can be substantial inter-annual variation in response to changes in

population density and food availability (Boyd *et al.* 1999). The sustained, low fertility rates (<70%) exhibited by harp seals since 1990 are notable. Some fur seal and sea lion populations sensitive to the variations in krill abundance and/or the effects of El Nino events have experienced sharp, shorter-term declines in reproductive success more extreme than harp seals, but usually not as sustained (e.g. Lunn and Boyd 1993; Trillmich 1993). In the case of the Barents Sea harp seal population, indirect analyses of fertility (using size-sequences of corpora) suggested a significant reduction in fecundity during the past 30 years (Kjellqwist *et al.* 1995). This conclusion was based on the observation that there has been an increase in the frequency of missing corpora in the ovaries of females collected from 1963 – 1972 (18.0%) to 1976-1985 (21.4%) and then to 1990-1993 (24.6%). Based on the same data, Frie *et al.* (2001) produced similar results using maturity curves fit to age specific proportions mature in each sample. Unfortunately, neither one of these analysis techniques are not directly comparable to the approach and data presented here. However, a fertility rate of 84% was obtained from a small sample of 32 females taken in early fall from 1990 -1993. This Barents Sea estimate is comparable to the Northwest Atlantic data and seems relatively high given the high estimate of MAM for the same period.

Eberhardt (1977) suggested that, in marine mammals, an increase of population density would affect fitness components in a predictable order; first juvenile survival, the fecundity of young females, then fecundity of adult females and last adult survival. The long-term changes in age specific pregnancy rates of females from 4 – 7+ years of age support this general hypothesis. Females 4 and 5 years of age exhibited more extreme changes in pregnancy rates that tended to increase and decline more rapidly and more sharply than older seals. It was this relatively abrupt increase in age specific pregnancy rates of 4 and 5 year old seals that strongly influenced the significant relationship between fertility rate and changes in the 1+ population presented by Bowen et al. (1981). However, determining which ecological factors were most important in causing this pulse of productivity during the early and mid 1980 is still problematic given that population size was increasing and there were significant changes in the marine environment. It is also difficult to assess the potential importance of low sample sizes during the 1980s. However, it is of interest to note that Gaillard *et al.* (2000), upon review the dynamics of ungulate populations, is of the opinion that Eberhardt's hypothesis can be generalized to other sources of temporal variation in population abundance (i.e. including climate-dependent food limitation or control by humans, predation and disease). This perspective supports the conclusion by Bowen *et al.* (1981) that monitoring changes in age specific pregnancy rate is a useful approach for gaining a better understanding of population dynamics and for developing population management initiatives regardless of whether the underlying mechanism is density dependent or not.

Age of Maturity

Although the changes in MAM were in the direction expected for a density dependant response, the magnitude of the more recent changes were inconsistent with changes in MAM during the 1950 -1980 period and the growth and size of the population from 1980 – 2001. The relationship between MAM and the changing size of the 1+ population lagged 5 years over the whole time series was extremely weak. This may have been in part due to the lack of the 1950s data, but perhaps more importantly, the population estimates and trajectory of population decline and growth estimated by the Healey and Stenson (2000) model are different from the Lett *et al.* (1978) and Winters (1978) models. The implications of this will have to be examined in future analyses. Also, the decline of MAM in the late 1970s and the subsequent increase in the late 1980s were both relatively abrupt or stepped; there is no obvious explanation for these observations except that for several of the years sample sizes were low and had to be combined. This lack of evidence for a density dependent response suggests that other ecological factors are important and that the relationship between population abundance and changes in reproductive potential are more complex. The relatively narrow ranges of variation in MAM over a time period when population size and the marine environment has changed significantly suggests this parameter is of limited value as an indicator of population dynamics. This is likely because the proportion of females pregnant in each age class has declined since 1980 and therefore, MAM has not changed significantly.

Mean age of sexual maturity varied from a low of 4.1 to a high of 5.8 y over the entire time series. This range is consistent with data from the Greenland Sea harp seal population where MAM has remained stable at 5.6 y from 1959 – 1990 (Frie *et al.* 2003). However, in the case of the Barents Sea harp seal population, MAM has varied from 5.4 – 8.2 y at various time periods between 1962 – 1993 (Frie *et al.* 2003; Kjellqwist *et al.* 1995). This is a considerably larger range of MAM than observed for either the Northwest Atlantic harp seal population or the Greenland Sea population. It is not clear if this difference has a physiological basis or perhaps is the result of an aging problem or a sampling bias. Given that the same personnel aged both the Greenland and Barents Sea samples as well as originally instructed Canadian personnel how to age teeth, it is not likely that an aging problem would account for all the observed differences. The calculation of MAM in all three populations is based on samples collected almost entirely (the Barents and Greenland Sea) or in part (Northwest Atlantic) from the spring moulting patches. As previously mentioned, temporal segregation of mature and immature seals maybe a potential problem at this time of year (Sergeant 1991; Oien and Oritsland 1995). Thus, if the difference is not physiologically based, perhaps this is where the root of the problem lies. Small sample sizes and differing analysis techniques (i.e. MAM based on the back calculation of ovarian structures) may also be contributing to the problem. However, Frie *et al.* (2003) has presented good comparative evidence that this is not the case. A possible biological explanation for the high MAM in the Barents Sea will be discussed later.

When Bowen *et al.* (1981) examined MAM in Northwest Atlantic harps seals he concluded that there was no statistical or biological reason why maturity data collected from January (winter) and April (spring moulting period) should not be used. Therefore, he used a spring, and winter sample for each year of the time series in the MAM regression analyses. For this study, all samples except those collected in March were combined and used as a single annual sample given the constrains of sample size during the 1980s. This difference in sample treatment is the primary explanation for the minor differences between the MAM estimates presented in Bowen *et al.* (1981) and data presented in this study. In the future it may be useful to compare the winter and spring samples from the post 1980 period in more detail. Perhaps, this might clarify whether or not a moulting patch sample bias is a plausible explanation for the differing range of MAM estimates observed between the Northwest Atlantic and the Barents Sea populations.

Potential Role of a Changing Marine Environment

Given that reproductive parameters of harps seals did not appear to be strongly influenced by population size, the potential importance of environmental factors need to be considered. Colder than normal water temperatures in the Northwest Atlantic from the late 1980s to mid 1990s (Colbourne 2002; Colbourne *et al.* 1994; Drinkwater 1996; 2002) are thought to have contributed to the significant changes in abundance, reproductive biology, distribution and habitat use of many demersal fish (Atkinson 1994; DFO 2002a; Drinkwater 2000; Gommes *et al.* 1995), pelagic fish (DFO 2000b and c; 2001; Lilley *et al.* 2000) and crustaceans (DFO 2002b and c; Parsons and Colbourne 2000). Of these many observed changes, the most important in terms of understanding the influence of the marine environment on seal reproductive potential may be those involving capelin (*Mallotus villosus)* and Arctic cod (*Boreogadus saida)* - key fish prey species for harp seals (Lawson et al. 1995; Lawson and Stenson 1997b). The likely mechanism of interaction may be the ecological links between seal growth and condition and changes in the distribution, availability and quality of these two prey species.

There is a large body of literature documenting the relationships between physical condition/growth and reproductive parameters of pinnipeds, particularly mean age of sexual maturity (eg. Laws 1956, 1959; Stewart and Lavigne 1984; Boyd 1991) and pregnancy rates (eg. Eberhardt 1977; Frisch 1978). Although data on body condition of harps seals in the Northwest Atlantic are limited, the observed long-term changes are consistent with the hypothesis that environmentally induced changes in the availability and/or quality of prey species could have negatively impacted harp seal reproductive potential. Chabot *et al.* (1996) showed that growth rates for young females (< 5 years old) sampled from 1990 -1994 were significantly slower than at any other period of time since 1976. The same study also indicated that young males weighed less and were shorter at a given age in 1990 -1994 (the time periods used for comparison were 1976 – 1979; 1980 –1984; 1985 – 1989; and 1990 - 1994). Older seals of both sexes

were in worse post breeding condition in 1992 that in the mid 1980s, but they did not differ from seals sampled in the early 1980s or mid 1970s period. More recently (1995 - 2002), there have been numerous reports from Newfoundland and Labrador fishermen that suggest juvenile harp seals from some areas of the Province are in poor condition (i.e. decreased blubber layer). Hammill *et al.* (1995) compared body condition of harp seals taken in the Gulf of St. Lawrence from 1976 – 1979 and from 1988 -1992. Seals from the later period were in poorer condition suggesting a decline in available resources, but he could not exclude the possibility of sampling bias.

Harp seals prey on a wide range of fish and crustacean species and their diet is known to vary geographically and seasonally (Sergeant 1991; Lawson *et al.* 1985; Lawson and Stenson 1997b). For these reasons it is difficult to make general interpretations regarding the affects of changing prey availability and/or quality on seal reproductive potential. However, early diet studies of harp seals indicated that capelin was by far the most important prey species consumed in Newfoundland waters and Arctic cod was the primary prey species taken in Arctic waters during the summer (Sergeant 1973; 1991). The availability of capelin is thought to be important during November to early March when seals are extensively feeding to maximize their body condition prior to the breeding season (Sergeant 1991; Chabot *et al.* 1996). This historical predominance of capelin and Arctic cod in the seasonal diet of seals, our knowledge of the schooling behavior, energy content and digestibility of these prey species, coupled with what is know about seal foraging and migratory behavior provides some insight into the complex suite of ecological factors that may be influencing available resources and seal reproductive potential. In terms of prey quality, capelin (pre-spawning) has one of the highest energy densities of any harp seal prey species (Lawson *et al.* 1998b) as well as optimal digestion efficiency (Lawson *et al.* 1997a). Arctic cod has an energy density that is significantly lower than pre-spawning capelin but similar to capelin in post-spawning condition; the digestion efficiency of Arctic cod is significantly lower that capelin regardless of geography and season. Lawson *et al.* (1998a) presented preliminary evidence that, when given a choice, harp seals in offshore areas preferentially selected capelin prey relative to other species regardless of their local abundance. Arctic cod was a preferred prey species in nearshore areas, but not in the offshore areas (Lawson et al. 1998a). These data establish the basis for a potential relationship between changing seal diet and the concept that increased consumption of a less digestible, lower energy prey species at times of the year when a high energy food source is required could have had a negative effect on body condition and perhaps growth (e.g. Hammill *et al.*1995).

An example of such a scenario occurred during the mid 1980s when offshore acoustic surveys indicated that capelin were scarce along the coast of Labrador and Grand Banks and then virtually absent by the early 1990s (Carscadden *et al.* 2001). In contrast, abundance increased on the Flemish Cap and on the Scotian Shelf indicating a southern shift in capelin distribution (Carscadden *et al.* 2001; Frank *et al.* 1996). Spawning times in coastal areas

were also more variable and significantly delayed during the 1990s (Lilly and Carscadden 2002; Carscadden and Nakashima 1997b; Carscadden *et al.* 1997a; Nakashima 1996). Concurrently, Arctic cod distribution shifted southward from Labrador waters into Newfoundland coastal areas and on to the Grand Banks and then eastward out to the continental shelf-edge; this notable expansion and increase in biomass peaked in about 1995 (Lilley *et al.* 1994; Lilly and Simpson 2000).

During this period of change in the distribution and abundance of key fish prey species, there were also examples of related shifts in harp seal distribution, habitat use and diet. From at least 1990 - 1995 Arctic cod became a significantly more important prey species for seals foraging in many nearshore areas off Newfoundland during the spring; Arctic cod had been the key prey species during the winter since 1986 (Stenson and Perry 2001). Reports from fisherman at the time indicated that during the 1990s seals were moving into Newfoundland nearshore waters earlier in the fall, staying later into the summer and foraging in coastal water habitats rarely frequented before (pers. comm. W. Penney, DFO). This rather abrupt increase in the importance of Arctic cod in the summer diet of seals coincides closely with reports of increased seal numbers in nearshore waters. This is noteworthy from a changing predator/prey distributional perspective; however, the predominance of Arctic cod in the winter diet since 1986 when traditionally capelin was more important (Sergeant 1991; Lawson and Stenson 1995), may be germane to understanding potential diet related changes in body condition and seal reproductive potential. Observations and reports of harp seals shifting their traditional distribution southward during the winter and early spring started occurring in the late 1980s (Stenson and Kavanagh 1993; Lacoste and Stenson 2000) and increased notably during the mid -1990s with seals frequenting the coast of Maine and as far south as New Jersey (Slocum *et al.* 1995; Stenson and Sjare 1997; Stevick and Fernald 1998; Warring *et. al.* 1999). There was also an increase in the number of harp seal strandings reported on Sable Island (Z. Lukas pers. com.). Again, there appears to be evidence for a predator/prey distributional shift, but unfortunately, available seal diet data for most offshore areas are limited and it is not possible to track whether the importance of capelin has changed during the 1980s and 1990s. Some portion of the seal population is continuing to consume capelin in offshore areas (Stenson and Perry 2001) despite the fact researchers have not been able to assess the abundance since the early 1990s. However, given these significant shifts in both predator and prey distribution in offshore areas, it is possible the availability of capelin for various components of the seal population may have changed significantly.

These concurrent observations of change in the distribution, abundance and likely availability of capelin and Arctic cod and the diets and distribution of harp seals substantiate the linkages between seal diet, body conditions and reproductive potential. Although the discussion has focused on capelin and Arctic cod, since the late 1990s the amount of sand lance (which has a relatively low energy density) has increased in the offshore diet while herring (which is

comparable to capelin in energy density) has increased in the nearshore diets; both species warrant further study in terms of understanding the changing marine environment and harp seal reproductive potential. These observations are insufficient to establish causal relationships in most cases, but they do suggest that large-scale changes in the Northwest Atlantic marine ecosystem during the mid 1980s to the late 1990s may have influenced the reproductive potential of female harp seals by reducing per-capita resource levels. Frie *et al.* (2003) has presented a parallel scenario for the Barents Sea harp seal population. The high estimate of MAM for seals in the Barents Sea (8.2 y) from 1988 -- 1993 coincided with the severe depletion of herring and capelin stocks and a highly variable abundance of Arctic cod stocks in the Barents Sea. It was also during this time that Barents Sea harp seals invaded the Norwegian coast (1986 – 1988). Haug and Nilssen (1995) suggested that the invasions resulted from food shortages due to the simultaneous low abundance of all three key pelagic forage fish species. There is some support for this hypothesis given that the body condition of seals caught in 1988, when capelin was depleted, was significantly reduced compared to seals caught in 1993, when capelin stocks were recovering (Haug and Nilssen 1995). Frie *et al.* (2003) considers that the severity of the food shortage for seals in the Barents Sea may be the most plausible explanation for the high estimates of MAM for that population.

Acknowledgements

We would like to thank Dave Mckinnon, Wayne Penney and Dennis Wakeham for their continued expertise and dedication both in the lab and in the field. We would also like to thank the many seal hunters and fishermen that have supported and participated in our biological sampling program over the years. Greatly appreciated statistical advice was provided by B. Warren and G. Robertson and constructive comments provided by the National Marine Mammal Peer Review Committee significantly improved this manuscript.

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Table 1. Ovulation rates of mature females 1954-2001.

Year	Sample size	Ovulation rate	SE
1954	82	0.976	0.017
1962	43	1.000	0.000
1966	65	1.000	0.000
1968	62	0.968	0.022
1976	85	0.988	0.012
1979	65	0.985	0.015
1981	32	0.969	0.031
1982	43	0.977	0.023
1983	130	0.985	0.011
1984	100	0.96	0.020
1986-87	42	0.857	0.054
1988-91	28	0.714	0.085
1992	109	0.972	0.016
1993	36	0.917	0.046
1994	44	0.909	0.043
1995	61	0.951	0.028
1996	75	0.973	0.019
1997	62	0.903	0.038
1998	219	0.959	0.013
1999	15	0.867	0.088
2000	206	0.995	0.005
2001	37	0.919	0.045

Table 2. Fertility rates of mature females 1954-2001.

Year	Sample size	Fertility rate	SE
1954	51	0.863	0.048
1964	32	0.844	0.064
1965	161	0.925	0.021
1966	59	0.983	0.017
1967	163	0.988	0.009
1968	85	0.929	0.028
1969	187	0.968	0.013
1970	116	0.948	0.021
1978	88	0.943	0.025
1979	51	0.941	0.033
1980	14	0.857	0.094
1981	29	0.862	0.064
1982	9	0.778	0.139
1985	10	0.700	0.145
1986	10	0.900	0.095
1987	44	0.705	0.069
1988	26	0.769	0.083
1989	31	0.935	0.044
1990	14	0.643	0.128
1991	36	0.722	0.075
1992	55	0.691	0.062
1993	47	0.574	0.072
1994	60	0.783	0.053
1995	37	0.676	0.077
1996	38	0.684	0.075
1997	43	0.814	0.059
1998	45	0.622	0.072
1999	81	0.580	0.055
2000	55	0.709	0.061
2001	43	0.698	0.07

Table 3. Age-specific pregnancy rates of females 1954-2001 (no. females pregnant/total number of females in sample).

	3 Years Old		4 Years Old		5 Years Old		6 Years Old		7 Years Old		8+ Years Old	
Year	n	Pregnancy rate	n	Pregnancy rate	n	Pregnancy rate	n	Pregnancy rate	n	Pregnancy rate	n	Pregnancy rate
1954	4	0	3	0.333	3	0.667	16	0.750	4	0.750	29	0.897
1964	11	0	9	0.111	2	0.500	4	0.750	5	1.000	20	0.850
1965	30	0.033	44	0.114	37	0.541	38	0.711	33	0.848	76	0.895
1966	7	0	9	0.111	17	0.353	11	0.727	8	0.875	41	0.878
1967	10	0	19	0.211	33	0.606	29	0.966	23	0.870	100	0.890
1968	27	0	19	0.316	20	0.700	12	0.917	11	0.818	44	0.886
1969	25	0.040	25	0.160	16	0.438	28	0.821	29	0.931	136	0.875
1970	13	0	13	0.231	12	0.500	10	0.900	19	0.947	88	0.841
1978	40	0.025	38	0.605	20	0.900	9	0.667	10	0.700	31	0.903
1979	21	0.238	15	0.533	5	1.000	9	0.889	4	1.000	17	0.941
1980	2	0	2	0.500	1	1.000	0		2	1.000	10	0.800
1981	5	0.200	4	0.750	2	0.500	7	0.857	0		17	0.824
1982	4	0	5	0.400	1	1.000	4	0.750	0		3	0.333
1985	4	0	3	0.333	5	0.400	3	1.000	0		1	1.000
1986	1	1	0	.	2	0.500	1	0.000	1	1.000	6	1.000
1987	12	0.167	8	0.375	9	0.778	4	1.00	1	1.000	23	0.609
1988	17	0.118	6	0.167	3	1.000	0	.	3	0.667	16	0.750
1989	8	0	9	0.111	6	0.500	3	1	2	1.000	20	1.000
1990	8	0	7	0.143	3	0.667	1	0	0	.	10	0.600
1991	10	0	11	0.182	7	0.571	3	0.333	3	0.333	26	0.692
1992	10	0.200	11	0.273	9	0.556	8	0.750	2	1.000	30	0.667
1993	11	0.091	17	0.118	7	0	5	0.800	3	0.667	32	0.563
1994	23	0.043	16	0.125	14	0.429	7	0.429	5	1	36	0.833
1995	10	0	13	0.462	4	0.500	5	0.400	0	.	24	0.625
1996	8	0	6	0	4	0.250	1	1	0	.	35	0.686
1997	6	0	4	0	10	0.300	2	1	2	1	34	0.824
1998	6	0	10	0.3	9	0.222	4	0.500	9	0.667	26	0.577
1999	6	0	7	0	18	0.222	15	0.400	9	0.778	50	0.600
2000	1	0	9	0.333	6	0.667	5	0.400	6	0.500	37	0.730
2001	2	0	0	.	2	1	3	0	3	1	36	0.694

Table 4. Estimated age specific pregnancy rates for females regardless of maturity status based on a kernel smoothing technique (Stenson *et al.* 2001).

Year	Age 3	Age 4	Age 5	Age 6	Age 7+
1954	0.0888	0.2863	0.6477	0.7944	0.8792
1955	0.0887	0.2535	0.628	0.7972	0.8791
1956	0.0886	0.2156	0.599	0.7999	0.8789
1957	0.0885	0.1831	0.5691	0.8025	0.8788
1958	0.0884	0.1625	0.5481	0.8049	0.8787
1959	0.0883	0.1527	0.5374	0.8072	0.8785
1960	0.0882	0.15	0.5335	0.8093	0.8783
1961	0.0881	0.1513	0.533	0.8113	0.878
1962	0.088	0.1546	0.5341	0.8131	0.8777
1963	0.0879	0.1591	0.536	0.8147	0.8774
1964	0.0878	0.1642	0.5381	0.8161	0.877
1965	0.0877	0.1698	0.5403	0.8172	0.8765
1966	0.0876	0.1758	0.5424	0.8182	0.8759
1967	0.0875	0.1823	0.5445	0.8188	0.8751
1968	0.0874	0.19	0.5464	0.8192	0.8742
1969	0.0873	0.2	0.5488	0.8193	0.8731
1970	0.0872	0.2146	0.5528	0.819	0.8717
1971	0.0872	0.2373	0.5607	0.8182	0.87
1972	0.0871	0.2727	0.577	0.817	0.8678
1973	0.087	0.3235	0.6081	0.8152	0.865
1974	0.0869	0.3859	0.6586	0.8127	0.8616
1975	0.0868	0.448	0.723	0.8096	0.8573
1976	0.0867	0.4975	0.7842	0.8055	0.8521
1977	0.0866	0.5289	0.8265	0.8006	0.8457
1978	0.0865	0.5439	0.846	0.7947	0.8381
1979	0.0864	0.5458	0.846	0.7878	0.8292
1980	0.0863	0.5367	0.83	0.7799	0.8191
1981	0.0862	0.5164	0.8	0.7711	0.8079
1982	0.0861	0.4833	0.7583	0.7614	0.7959
1983	0.086	0.4363	0.7101	0.7511	0.7836
1984	0.0859	0.3787	0.6624	0.7403	0.7713
1985	0.0858	0.3193	0.6202	0.7293	0.7595
1986	0.0857	0.2683	0.584	0.7183	0.7485
1987	0.0856	0.2312	0.5516	0.7077	0.7385
1988	0.0855	0.2075	0.5206	0.6974	0.7297
1989	0.0854	0.194	0.4903	0.6878	0.722
1990	0.0853	0.1873	0.4613	0.6788	0.7156
1991	0.0852	0.1847	0.4348	0.6706	0.7102
1992	0.0851	0.1844	0.4117	0.6632	0.7057
1993	0.085	0.1853	0.3926	0.6565	0.702
1994	0.0849	0.1866	0.3773	0.6506	0.6991
1995	0.0848	0.1876	0.3653	0.6454	0.6967
1996	0.0847	0.1882	0.356	0.6408	0.6948
1997	0.0846	0.188	0.3485	0.6369	0.6934
1998	0.0846	0.1868	0.3424	0.6335	0.6923
1999	0.0845	0.1847	0.3372	0.6306	0.6915

Table 5. Mean age of sexual maturity (MAM) 1954-2001.

Year	n	Mean	Var	LCL	UCL
1954	211	5.8	0.02	5.53	6.10
1962	89	4.9	0.07	4.35	5.43
1964	75	4.8	0.02	4.48	5.07
1965	283	5.6	0.02	5.38	5.89
1966	233	5.8	0.02	5.55	6.14
1967	235	5.4	0.02	5.09	5.62
1968	169	5.2	0.03	4.81	5.49
1969	284	5.6	0.03	5.26	5.96
1970	291	5.1	0.03	4.74	5.37
1976	155	5.2	0.12	4.50	5.89
1978	193	4.7	0.02	4.38	4.96
1979	131	4.1	0.03	3.77	4.43
1980	38	4.5	0.25	3.49	5.51
1981	195	4.7	0.06	4.18	5.17
1982	119	4.7	0.01	4.45	4.85
1983	192	4.6	0.01	4.35	4.82
1984-85	149	4.5	0.04	4.15	4.91
1986-87	225	4.6	0.04	4.16	4.97
1988	110	5.5	0.07	4.99	6.02
1989-90	170	5.3	0.03	5.03	5.65
1991	107	5.5	0.08	4.91	6.04
1992	379	5.4	0.02	5.05	5.67
1993	248	5.5	0.06	5.00	5.96
1994	240	5.4	0.04	5.06	5.82
1995	234	5.7	0.03	5.36	5.99
1996	211	5.5	0.06	5.06	6.00
1997	255	5.6	0.02	5.31	5.81
1998	392	5.4	0.02	5.11	5.72
1999	178	5.6	0.03	5.27	5.99
2000	432	4.9	0.02	4.54	5.16
2001	173	5.3	0.06	4.86	5.83

Table 6a. Relationship of mean age of sexual maturity with year and 1+ population size lagged 5 and 10 years only including data from 1965-1979.

	Slope	Intercept	R^2	F	P
Year	-0.0617 ± 0.0017	126.8 ± 3.4	0.372	1267	0.0001
1+ POP_{t-5}	1.26 ± 0.09	3.24 ± 0.15	0.083	179	0.0001

Table 6b. Relationship of mean age of sexual maturity year with and 1+ population size lagged 5 and 10 years only including data from 1980-2001.

	Slope	Intercept	R^2	F	P
Year	0.0385 ± 0.002	-71.57 ± 1.90	0.288	1635	0.0001
1+ POP_{t-5}	0.196 ± 0.008	4.54 ± 0.03	0.138	562	0.0001
1+ POP_{t-10}	0.201 ± 0.010	4.67 ± 0.03	0.107	419	0.0001

Table 6c. Relationship of mean age of sexual maturity and 1+ population size, lagged 1 to 10 years, 1962-2001.

	Slope	Intercept	R^2	F	P
Year	-0.0017 ± 0.004	8.50 ± 0.85	0.002	14.8	0.0001
1+ POP_{t-1}	0.068 ± 0.005	5.03 ± 0.02	0.035	208	0.0001
1+ POP_{t-2}	0.069 ± 0.005	5.03 ± 0.02	0.036	209	0.0001
1+ POP_{t-3}	0.071 ±0.005	5.03 ± 0.02	0.035	199	0.0001
1+ POP_{t-4}	0.071 ± 0.005	5.04 ± 0.02	0.032	186	0.0001
1+ POP_{t-5}	0.078 ± 0.006	5.02 ± 0.02	0.034	194	0.0001
1+ POP_{t-6}	0.114 ± 0.006	4.93 ± 0.02	0.065	358	0.0001
1+ POP_{t-7}	0.168 ± 0.006	4.79 ± 0.02	0.119	67[illegible]	0.0001
1+ POP_{t-8}	0.194 ± 0.007	4.73 ± 0.02	0.139	763	0.0001
1+ POP_{t-9}	0.215 ± 0.008	4.70 ± 0.02	0.148	794	0.0001
1+ POP_{t-10}	0.270 ± 0.008	4.57 ± 0.02	0.206	1105	0.0001

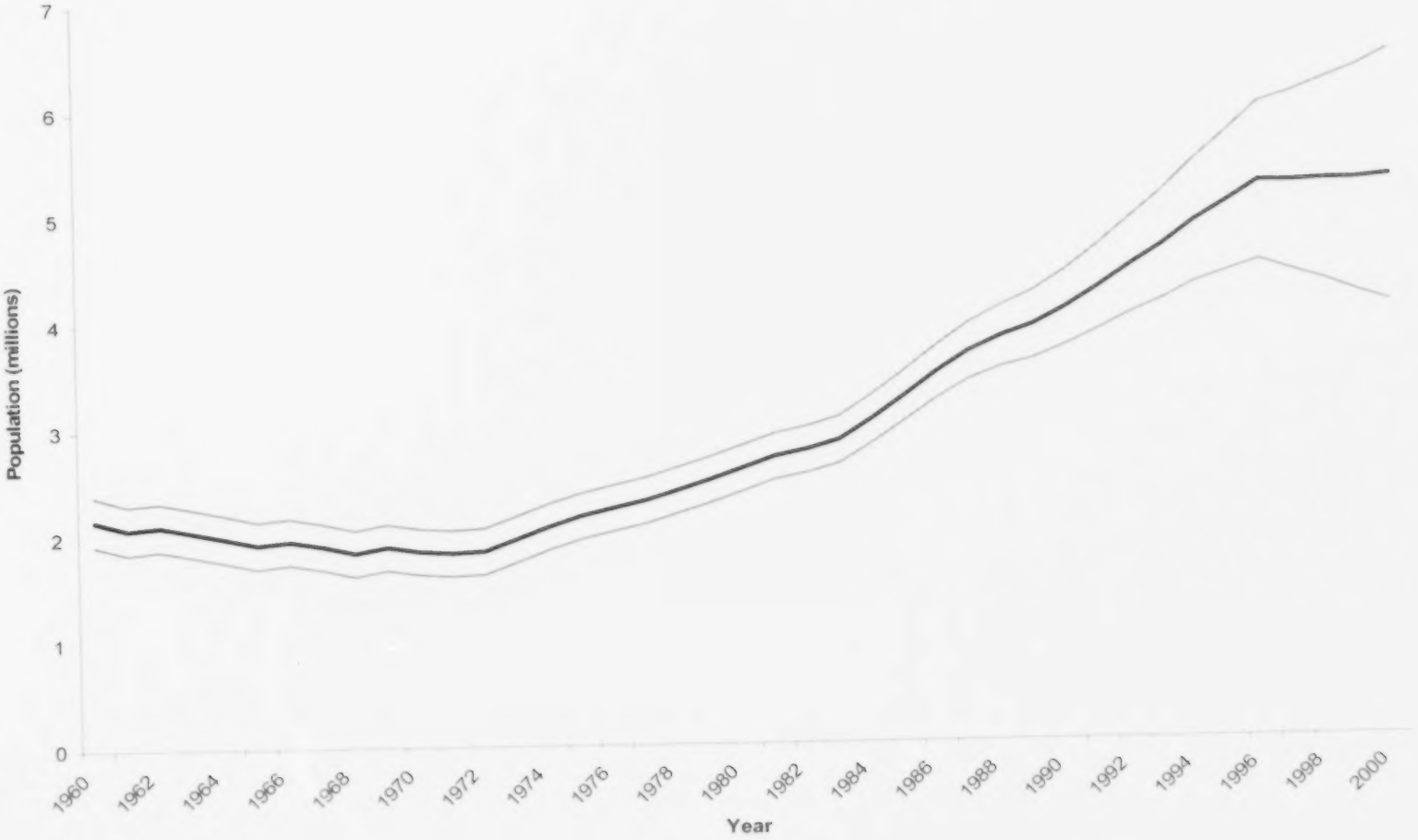

Figure 1. Population estimates (± 95% confidence interval) for Northwest Atlantic harp seals.

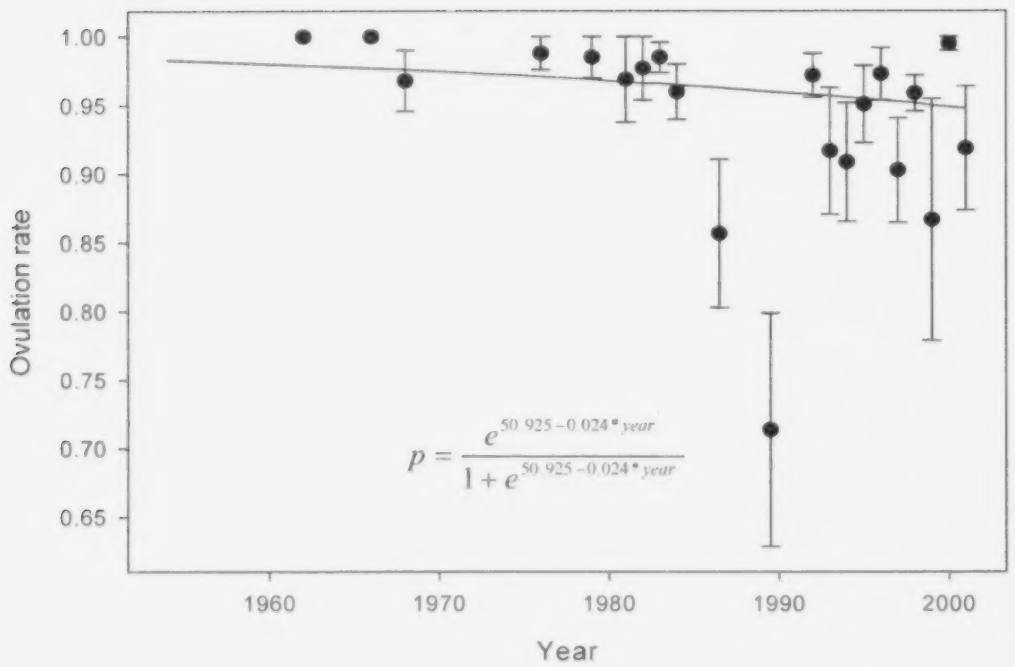

Figure 2. Ovulation rates (± 1 SE) of mature females across years (logistic regression, $\chi^2 = 4.92$, d.f. = 1, $P = 0.027$).

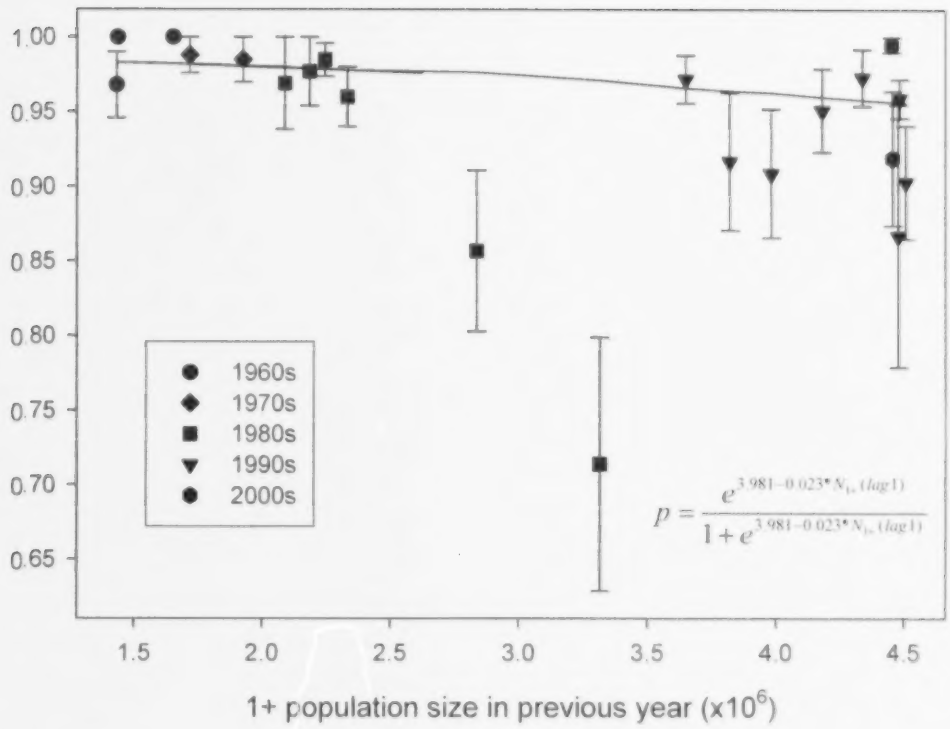

Figure 3. Ovulation rates (± 1 SE) of mature females against 1+ population size in previous year (logistic regression, $\chi^2 = 4.10$, d.f. = 1, $P = 0.043$).

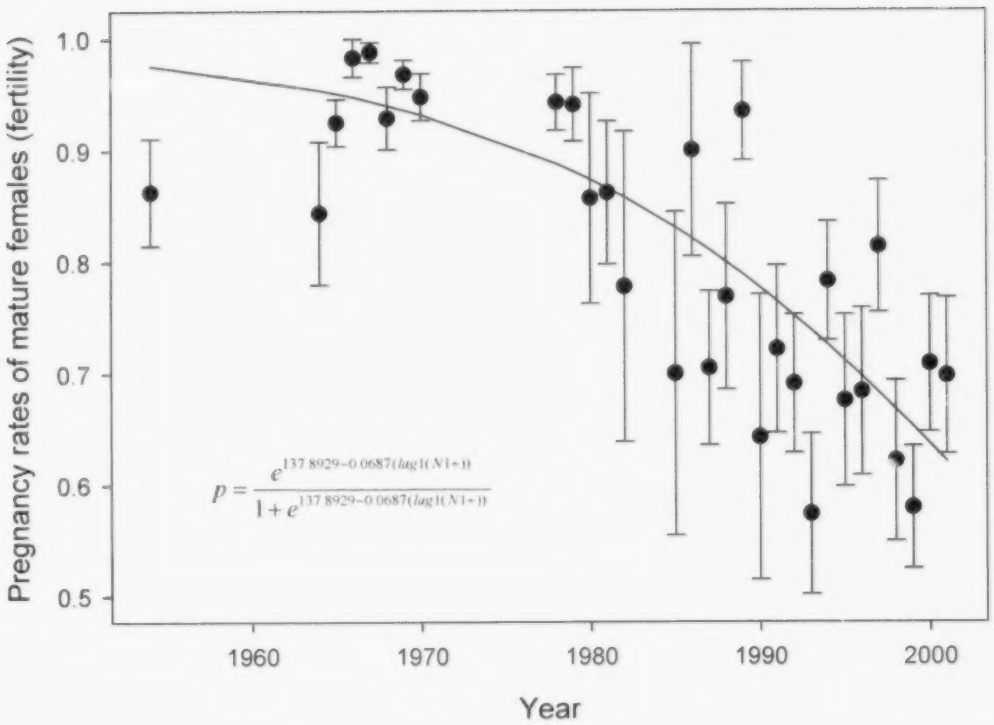

Figure 4 . Decline in fertility rates among mature females with year (logistic regression, $\chi^2 = 171.56$, P = 0.0001)

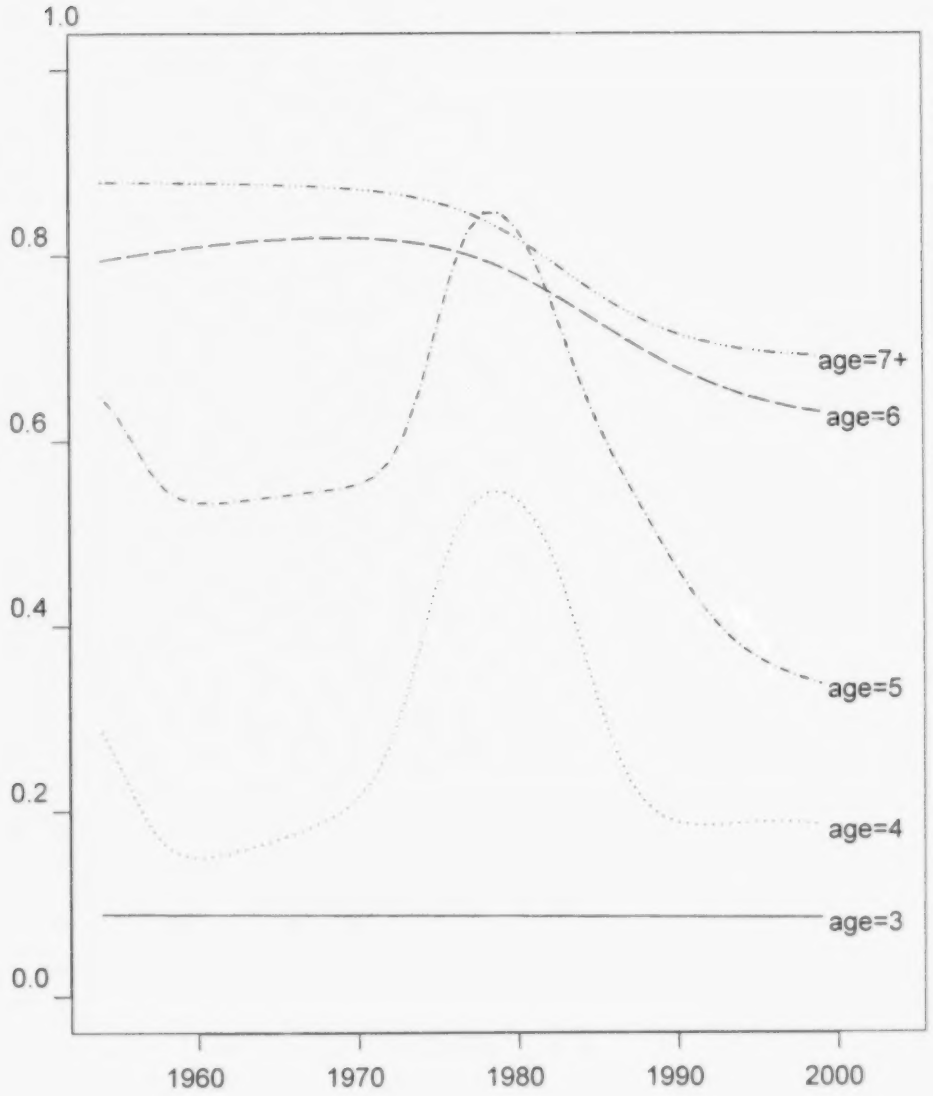

Figure 5. Estimated age specific pregnancy rates based on a kernel smoothing procedure (Healey *et al.* 2000).

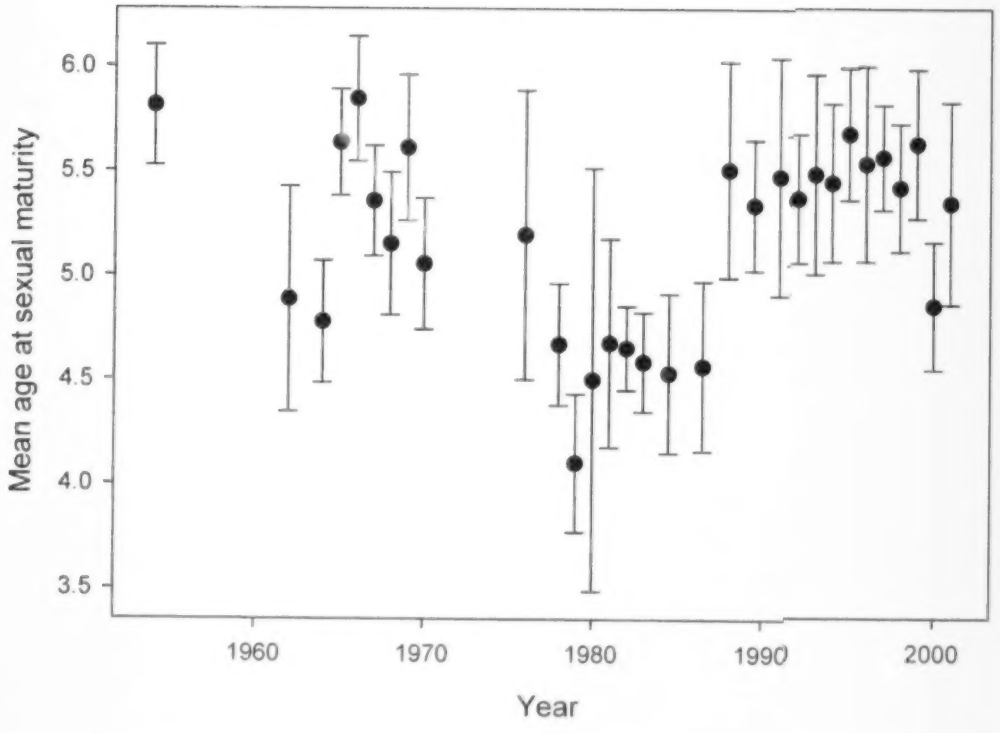

Figure 6. Changes in mean age of sexual maturity (± 95% CL) with year 1954-2001.

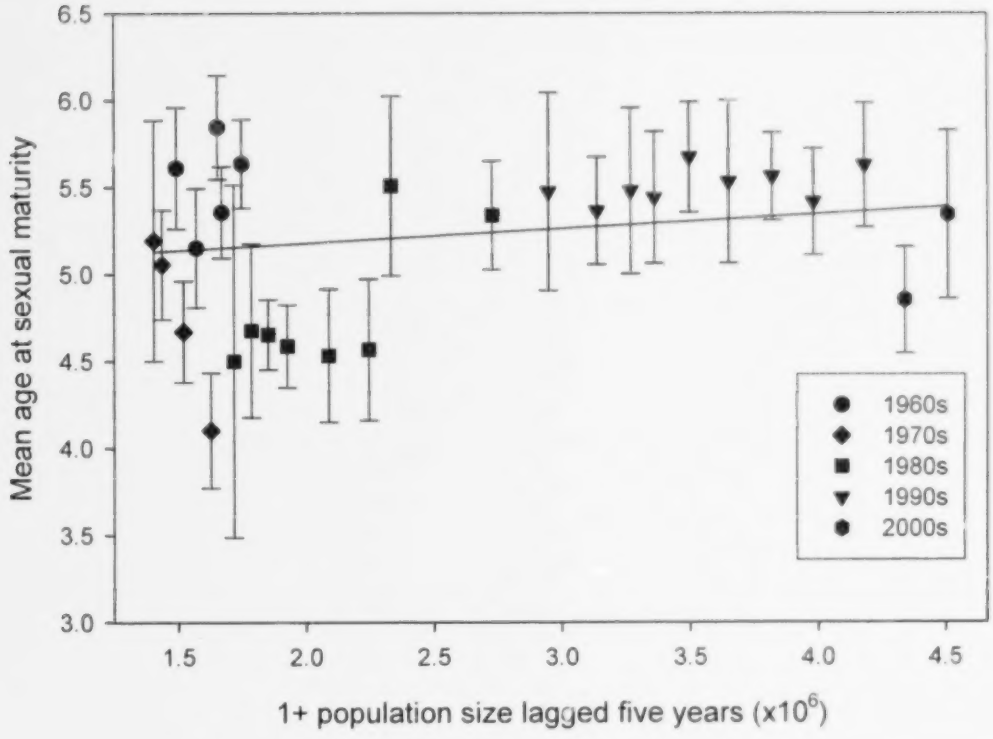

Figure 7. Mean age at sexual maturity (± 95% CL) and 1+ population size lagged 5 years, 1965-2001.

Appendix 1.

Nonparametric regression estimator for age specific pregnancy data:

Description of the nonparametric regression estimator used to estimate the expected pregnancy rates. There are no data for many year-age combinations, thus these expectations have to be inferred from neighboring observations using a simple model. We assume that for each age the number of pregnant seals sampled in year t (denoted as Y_t) from a total of n_t is Binomially distributed, with mean $n_t p_t$ where p_t is the probability that a seal was pregnant. With no further restrictions on p_t, the maximum likelihood estimate (mle) of p_t is y_t / n_t - the sample proportion of pregnant seals.

The sample proportion of pregnant seals may be quite dissimilar from year to year; however, we do not expect the population pregnancy rates to vary widely from year to year. Sample proportions may vary widely when the sample size is small, and this is compounded when there is considerable within-age population variability in sampled pregnancy rates. Another problem is estimating pregnancy rates in the years with no samples. These problems suggest that some reasonable model restrictions of the p_t's are necessary, especially to infer p_t's in years not sampled. Our approach is to borrow pregnancy information from "neighborhood" samples.

A common assumption that is reasonable in our case is that the p_t must be a smooth function of t. The amount of smoothness will be determined by the available data. The statistical problem then is to estimate this function or, equivalently, to estimate p_t. We cannot directly proceed to estimate p_t via maximum likelihood without specifying this function more exactly, which we do not want to do in our analysis, so a non-parametric approach is taken. Local averaging is a commonly used alternative to estimate p_t. The rationale for local averaging is as follows. Define an ε-neighborhood of observations around some given year t as $A_t = \{i : |t_i - t| \leq \varepsilon\}$. If ε is chosen small enough then we can assume that $p(t_i) = p(t)$ for all i in A_t. In this case the mle for $p(t)$ is:

$$\hat{p}(t) = \frac{\sum_{t_i \in A_t} y_i}{\sum_{t_i \in A_t} n_i}.$$

Only y_i's with t_i values within the ε - distance of t have a full contribution to the estimate of $p(t)$. Other y_i's have no contribution to the estimate. Another approach is to use a weight function designed so that the contribution of y_i changes gradually according to the distance between t_i and t. The weight function W measures the distance between t and t_i. The size of the neighborhood is determined by a bandwidth, b. The maximum local likelihood estimate (lle) is:

$$\tilde{p}(t) = \frac{\sum_i W\left\{\frac{(t_i - t)}{b}\right\} y_i}{\sum_i W\left\{\frac{(t_i - t)}{b}\right\} n_i}.$$

The Gaussian weight function, $W(x) \propto \exp(-x^2/2)$, is used here, although other functions are commonly used. The Gaussian weight function defines elliptical neighborhoods in t. As $b \to 0$, the neighborhood includes just t_i.

The choice of bandwidths is critical in smoothing. A bias-variance trade-off exists in determining the size of the bandwidths. A small bandwidth leads to an estimator with small bias but large variance (i.e. erratic), while a large bandwidth leads to an estimator with large bias but small variance (i.e. oversmooth). We use the data to choose the bandwidth, or the amount of smoothness. We find the bandwidth that minimizes a measure of prediction error. The measure we use is Generalized Cross Validation. This is a common prediction error measure used in kernel smoothing and spline smoothing. A fairly basic description of this measure is given in Hastie and Tibshirani (1990), along with comparisons with other methods. We feel that the amount of smoothness that is useful will depend on age, so we choose bandwidths separately for each age.